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ON THE "PAPILLOSE" ACHENES IN THE GENUS ANTENNARIA

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THE Old World and, consequently, the longest known species: *Antennaria dioica* (L.) Gaertn., *A. alpina* (L.) Gaertn. and *A. carpathica* (Wahl.) Bl. & Fingerh. and their remarkably few trifling aberrations have GLABROUS achenes. This fact has been stated in a few works. Most of the floras and descriptive books, however, do not mention the achenes of *Antennaria* at all; even "old faithful" HARTMAN, who generally in his Handb. Skand. Fl. 11 Edit. Stockholm 1879 gives a brief but fairly correct description of seeds and achenes where nobody else does so, fails here. In North America, where during the last thirty years about 150 new species have been detected and described by such writers as E. L. GREENE, M. L. FERNALD, P. A. RYDBERG, E. NELSON and others and where, accordingly, suitable characters for discerning the often difficult species would seemingly be needed, even the modern floras and handbooks content themselves in stating that the achenes of *Antennaria* are "terete or nearly so." This is curious since the great majority—if not all—of the species in the Atlantic States of U. S. A. have very distinct granular papillae on their achenes, by which character alone the long lasting confounding of American species with the Old World *A. dioica* might have been avoided.

Yet, papillose achenes in *Antennaria* have in some cases been mentioned by American botanists. The following list is probably very incomplete, owing to the present writer's lack of access to the literature. We find:

1897. Pittonia III. 173. *A. NEGLECTA* Greene described as having achenes "copiously papillose."
 174. *A. HOWELLII* Greene "papillose granular."
 175. *A. PEDICELLATA* Greene "very minutely and sparsely granular."
 184. *A. NEODOICA* Greene "rather coarsely and obviously granular."
 1898. 277. *A. "PLANTAGINIFOLIA"* (= *A. PARLINII* Fern.) "nearly destitute of papillae."
 1903. Pittonia V. 111. *A. MESOCHORA* Greene "globular papillose."
 1921. RHODORA XXIII. 295. *A. APPENDICULATA* Fern. "papillose."
 1924. RHODORA XXVI. 102. *A. SUBVISCOSA* Fernald "papillose."
A. ISOLEPIS Greene "sparingly papillose" (*Fernald*).

Thanks to the courtesy of Professor FERNALD I have been able to investigate a large number of the Atlantic American species of *Antennaria* in well authenticated specimens. I shall here enumerate the cases where I have noticed papillose achenes, as some of them seem not to have been mentioned before.

A. PARLINII Fern. (*A. arnoglossa* Greene). North Berwick, Me., June 12, 1897, *J. C. Parlin*, (2 sheets); Orono, Me., May 30, 1901, *M. L. Fernald* (2 sheets).

Achenes at full maturity (N. Berwick plant) rather large, 1.79–2.07 mm. long, 0.42–0.50 mm. broad. Papillae evenly dispersed over the whole surface, but rather small. (FIG. 1, a.)

A. CANADENSIS Greene, toward var. *RANDII* Fern. Farmington, Me., June 20, 1897, *C. H. Knowlton*.

Achenes not quite mature, $1.20\text{--}1.40 \times 0.34\text{--}0.42$ mm. Papillae as in above, probably somewhat larger. (FIG. 1, b.)

A. PLANTAGINIFOLIA (L.) Richards. Stoneham, Mass., May 23, 1895, *W. P. Rich.*

Achenes very young, but evidently papillose.

A. NEODOICA Greene. Wells Beach, Me., June 22, 1898, *Kate Furbish*.

Achenes mature, $1.29\text{--}1.46 \times 0.34\text{--}0.39$ mm. Papillae slightly scarcer in number and longer than in the preceding.

A. NEODIOICA var. *RUPICOLA* Fern. Island Falls, Me., June 9, 1898, *M. L. Fernald*.

Achenes quite young, but distinctly papillose.

A. NEODIOICA var. *GASPENSIS* Fern. Gaspé Co., Qué., *Pl. Exsicc. Gray*. 291.

Achenes immature, rather sparingly papillose.

A. NEODIOICA var. *GASPENSIS* Fern. Mt. Pembroke, Matane Co., Que., July 16, 1923, *Griscom & Pease*, 26,058.

Achenes immature, but copiously papillose.

A. PETALOIDEA Fern. Foxcroft, Me., June 6, 1898, *M. L. Fernald*, 2390 (2 sheets).

Achenes well mature, $1.48\text{--}1.60 \times 0.39\text{--}0.48$ mm., papillose; Harwich, Mass., May 11, 1919, *Fernald*, 19,243: mostly male specimens, one immature pistillate papillose. (FIG. 1, c.)

A. PETALOIDEA var. *SUBCORYMBOSA* Fern. Pr. Edw. Isl., June 29, 1914. *Pl. Exsicc. Gray*. 292.

Achenes well matured, papillose.

A. PETALOIDEA var. *SCARIOSA* Fern. Orono, Me., June 3, 1898, *M. L. Fernald*.

Achenes nearly mature, papillose. Same locality, May 30, 1901, *M. L. Fernald*. Achenes immature, papillose.

A. SPATHULATA Fern. St. Johns Island, Newfdl., July 31, 1925, *Fernald et al.*, 29,183.

Achenes mature, $1.23-1.37 \times 0.36-0.42$ mm., often somewhat angled; base of style longer than in other species, up to 0.20 mm. long; achenes papillose (FIG .1, d.).

A. SPATHULATA var. *CONTINENTIS* Fern. & St. John. Burnt Cape, Newfdl., July 17, 1925, *Fernald et al.*, 29,184.

Achenes nearly mature, papillose.

As will be seen, all the species here enumerated as well as most of those stated by Greene to have papillose achenes belong to the large-sized groups of species flocking around *A. plantaginifolia* or around *A. canadensis* or *A. neodioica*. Of the small sized species from localities abundant in Arctic types, FERNALD states l. c. as having *glabrous* achenes: *A. ALPINA* (L.) Gaertn (!); *A. SORNBORGERI* Fern.; *A. CANA* (Fern. & Wiegand) Fern. (several sheets!); *A. ALBICANS* Fern. (!); *A. STRAMINEA* Fern.; *A. PEASEI* Fern.

Of the species marked by a (!) I can but verify this statement as shown by specimens kindly sent me by Professor FERNALD. And to the series I can add *A. vexillifera* Fern. from a part of the type collection.

Of *A. straminea* I have not seen the type described in 1914 and redescribed in 1924, RHODORA xxvi. 100, in which last place the achenes are said to be glabrous. But a later collection, also from Newfdl. *Fernald et al.*, 27,187 contains specimens with well matured achenes, $1.40-1.46 \times 0.42-0.45$ mm. which are very distinctly papillose. Because of the real nature of the “papillae” which will be treated subsequently, I can hardly think that the same species may sometimes have and sometimes lack that character, so there seems to be some mistake in one of the two collections.¹

Of the species of *Antennaria* thus far known to me from Greenland I have seen papillose achenes in two species, one of which is a rather stout plant seen in a large number of specimens from about 10 localities in West Greenland, ranging from 66° – 71° Lat. N. and which I have supposed to be conspecific with *A. subviscosa* Fern., but which Professor FERNALD is treating as a Greenland endemic, *A. affinis* Fern. The other is a dwarfish species from the southernmost parts in

¹The type of *A. straminea* has glabrous achenes.—M. L. F.

Greenland and in the field confounded with *A. groenlandica* Porsild, the most common *Antennaria* species in this section. I am unable to identify it; it is probably a new species.

Antennaria species of Greenland with glabrous achenes are *A. alpina* (L.) Gaertn., *A. angustifolia* Elis. Ekman, *A. glabrata* (Vahl) Greene, *A. intermedia* (Rosenv.) Porsild, *A. groenlandica* Porsild, *A. Porsildii* Elis. Ekman and two or three still unidentified species resembling Fernald's species *A. vexillifera*,¹ *A. cana* and *A. albicans* respectively.

From the Rocky Mountains of Alberta I have 7 sheets of *Antennaria*, kindly presented by Dr. M. O. MALTE. They represent, I think, 4 or 5 species, but they are unknown to me. All have glabrous achenes.

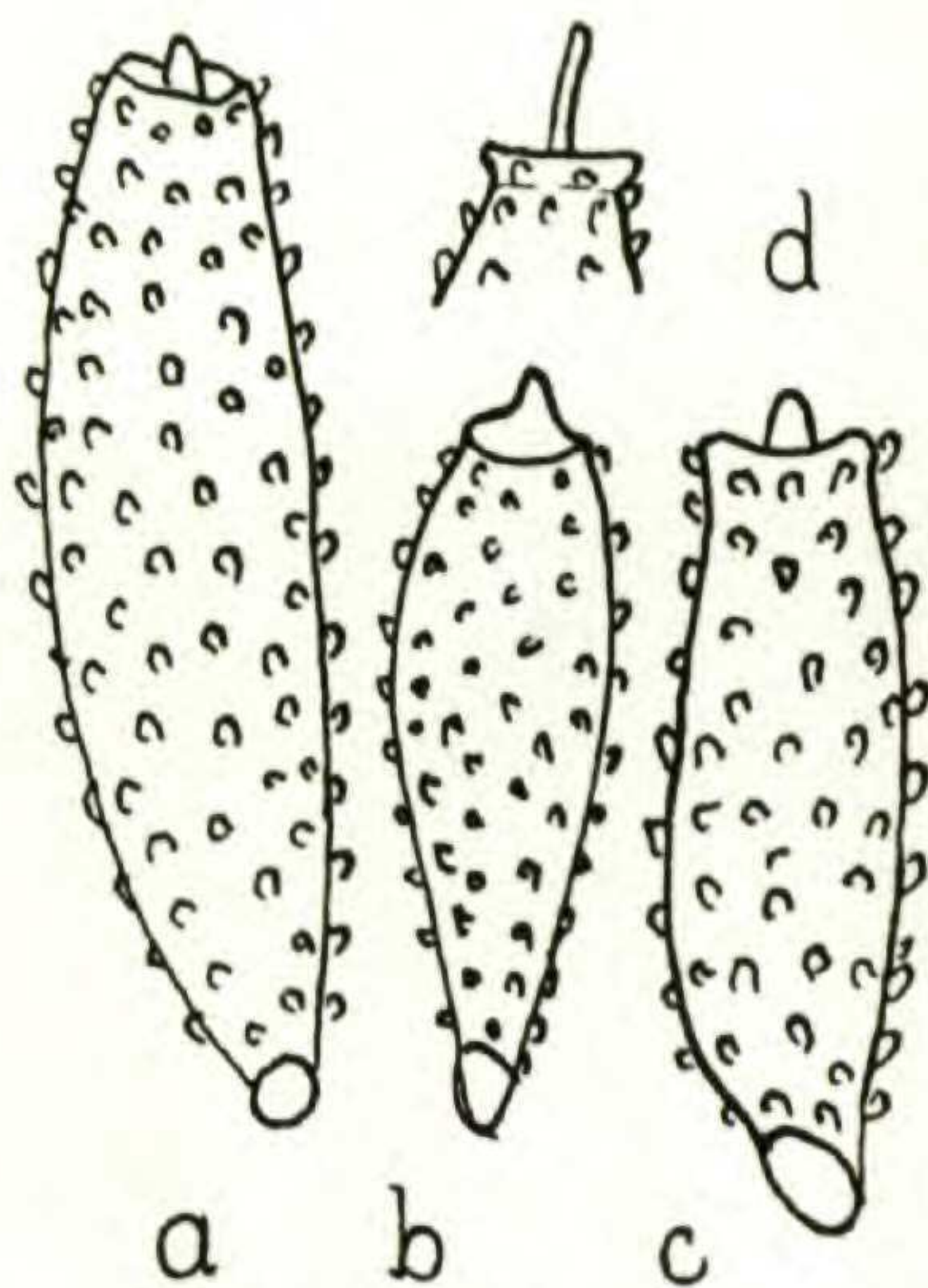


Fig. 1. Mature Achenes of *a*: *ANTENNARIA* *PARLINII*; *b*: *A. CANADENSIS*; *c*: *A. PETALOIDEA*; *d*: *A. SPATHULATA*; all $\times 16$.

At full maturity the achenes of all the *Antennarias* investigated are very much alike as to form (FIG. 1.) They are terete, slightly tapering towards both ends so that the largest diameter is generally in the upper half. The pappus-bristles are united into a very short tube, breaking off as a whole and leaving an annular crown in the center of which the base of the style remains as a projecting short pointed tip. The outer wall of the achene is brownish with a faint fatty lustre. The cells of the epidermis are thick-walled, narrow, with square ends, forming regular longitudinal series. At the lower end of the achene is a globular nodule of thick-walled, uncolored cells, forming the part inserted in the pits of the receptacle.

¹ *A. BREVISTYLA* Fern., published in this issue.—M. L. F.

When “papillae” are present, they are uniformly dispersed from the nodule to the pappus-crown. In the species there are small variations in the length and the density of the papillae from species to species, whereas they are remarkably uniform in the same head. Still I doubt that a species can be identified from these variations alone. On the dry and mature achene they appear as hyaline reflecting granules, easily seen by enlargements from 25 times upwards.

When the achenes are thrown into water they are only with difficulty wetted but will float for a long time. Still when they, after treating with a soft brush, are forced down, their specific gravity is shown to be greater than that of water. Having been soaked in water for 24–48 hours the “papillae” project well out from the surface as short gland-like hairs, bifurcated at the top. This result can be obtained more rapidly by placing the achenes in solutions of caustic soda or of chloral hydrate, or, better still, by placing the dry achenes directly in chloriodine of zinc. After a couple of hours they will have swelled,

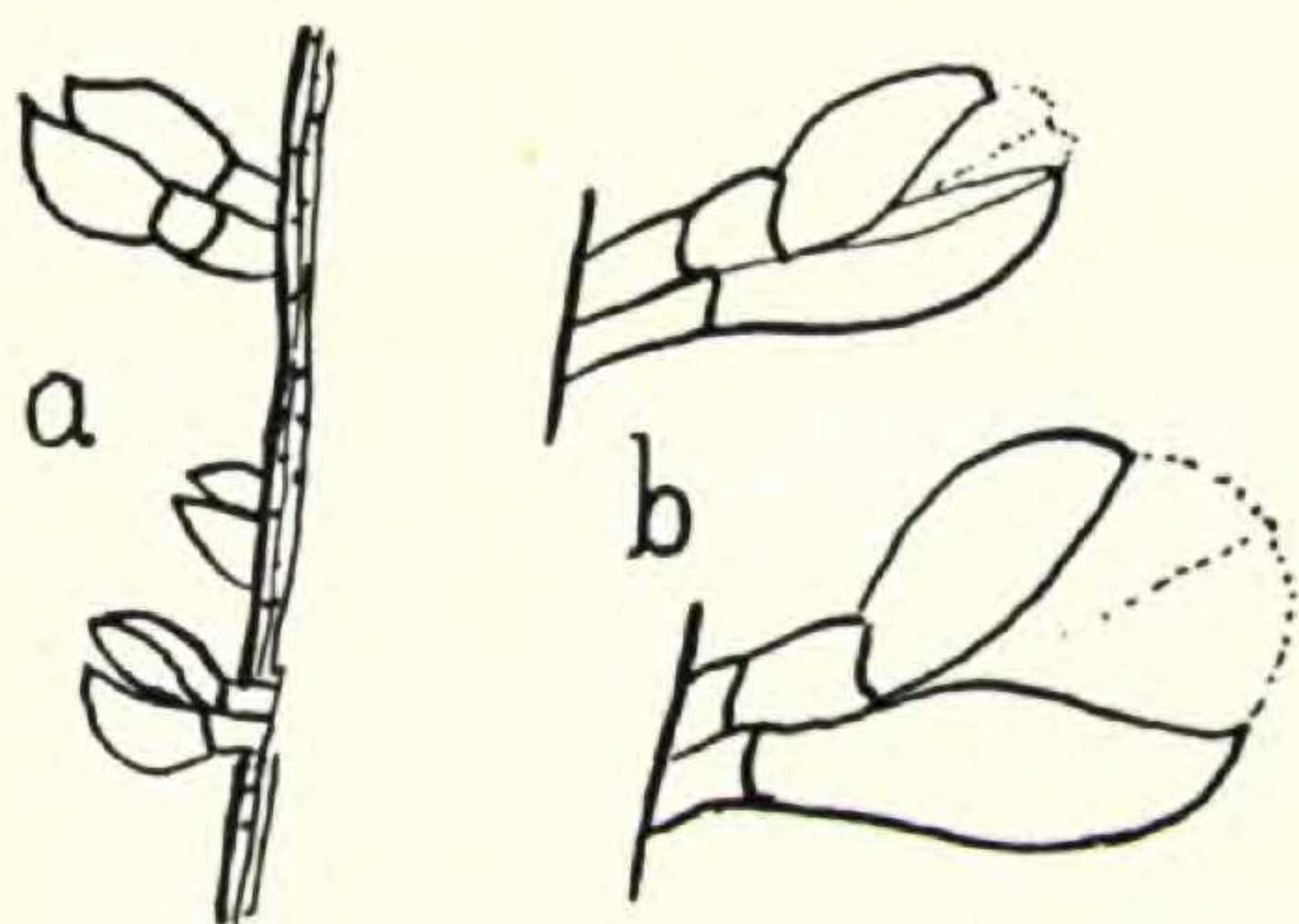


Fig. 2. Achenial Hairs swollen, *a*: of *ANTENNARIA PETALOIDEA*, $\times 133$; *b*: *A. NEODIOICA*, $\times 265$, showing drops of mucilage.

their upper halves then being stained blue, the lower light yellow, contrasting well with the brown wall-cells. In strong solutions of chloral hydrate the terminal cells will finally distend to nearly a right angle. The forms of the hairs of the mature achenes will appear from FIGURES 2, *a* and *b*. They are essentially identical for all species investigated. They are always slightly directed upwards, and the lower terminal cell is always larger than the upper. In one instance I have seen a globular drop of mucilage in nearly all hairs on some half a dozen achenes contained on one slide, but unfortunately I have not been able to repeat the observation (FIG. 2, *b*). As plant mucilages generally have the same refraction exponent as water or watery solutions and as they are not colored with ordinary chemicals, they are always somewhat difficult to see. As, according to MOLISCH:

Mikrochemie der Pflanze. Jena 1913 p. 314, mucilage may be dissolved by chloral hydrate, this substance should be avoided where the occurrence of mucilage is studied.

These hairs evidently represent a form of the curious and very polymorphous *duplex hairs* or *twin hairs* occurring on the achenes of a great number of genera of the *Compositae*. In spite of the fact that these very peculiar organs with their still hardly understood functions (if any, some secreting mucilage, others containing elastic spires, elaters) seem to occur in all tribes of the *Compositae*, so as to be simply a main character for the whole family, they are generally not mentioned in the handbooks, either of taxonomy or of anatomy, not even in the elaborate treatment of the family by HOFFMANN in ENGLER & PRANTL, Pflanzenfamilien. An exception is HEGI's Illustrierte Flora von Mittel-Europa, VI.¹ p. 399, where a brief description, illustrated by some figures from a paper of HANAUSEK is given.

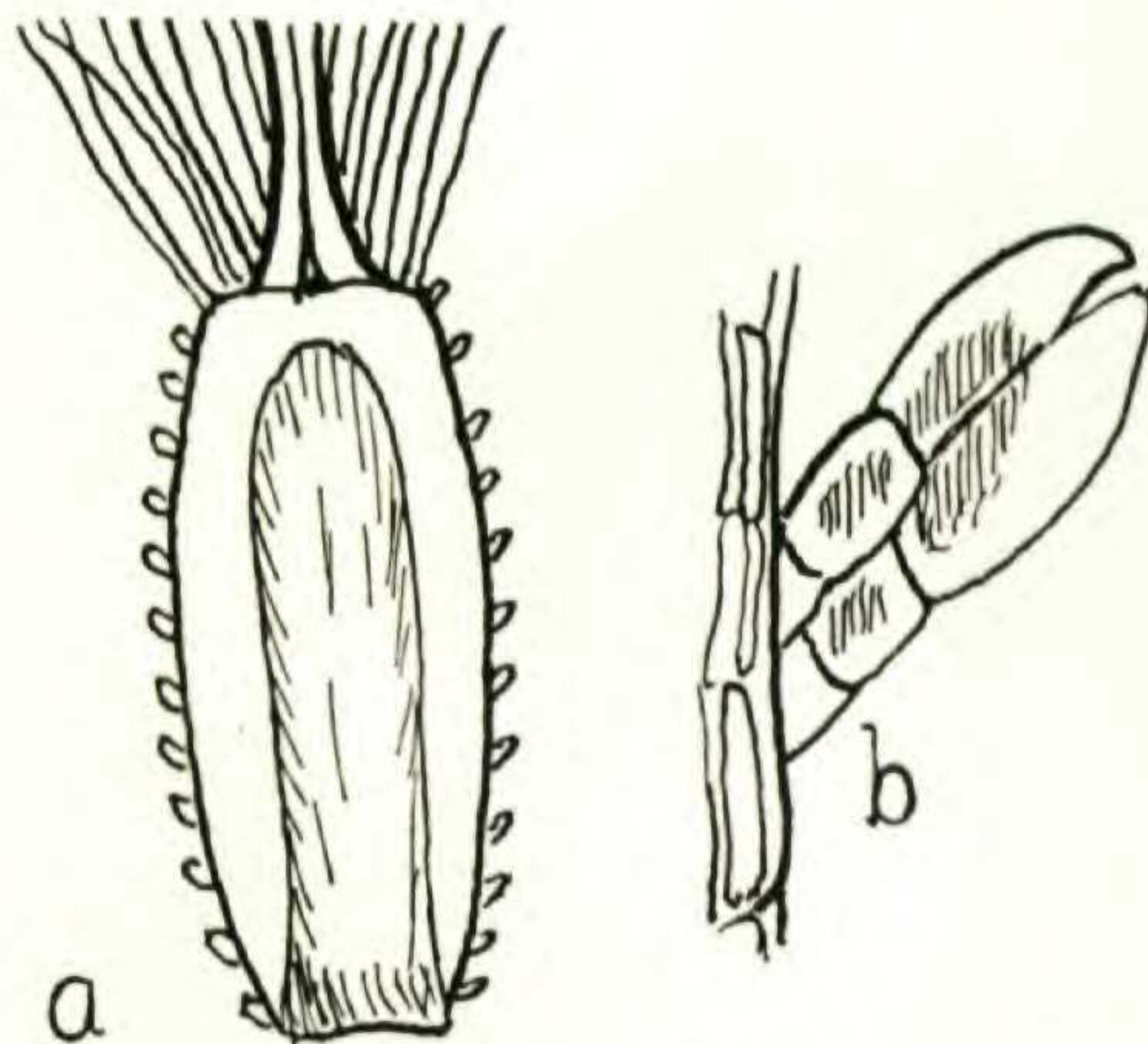


Fig. 3. *a*: Young Ovary of *ANTENNARIA NEODIOICA*, var. *GASPENSIS*, shown in optical section, $\times 16$; *b*: achenial hairs, showing cell-contents, $\times 265$.

In his most valuable and suggestive work "The Origin and Development of the *Compositae*" JAMES SMALL gives¹ a brief but clear account of the principal types of twin-hairs and their occurrences in the generally adopted tribes of the *Compositae*. He also gives a bibliography reaching from 1861 to 1912, to which may be added: HANAUSEK: Zur Entwicklungsgeschichte d. Perikarps v. *Helianthus annuus*. Ber. D. Bot. Ges. 20. 1902. Professor SMALL and most of the previous writers quoted by him seem to ascribe to the twin-hairs great value as bearing on evolutionary questions.

¹ J. Small, New Phyt. xvii. 72 et seq. 1918.

The hairs on the achenes of the *Antennarias* are nearly developed before the heads and the corollas expand. In lack of alcoholic material herbarium specimens will easily show them after a boiling in water, with a few drops of chloral hydrate added, and a subsequent transferring into alcohol for hardening. FIGURE 3, a, shows quite young and transparent achenes of *A. neodioica* var. *gaspensis* and FIG. 3, b, one of the hairs still with contents in the cells.

In dealing with the twin hairs of the *Compositae* HEGI says l. c. p. 399: “In vielen Fällen sondern die verdickten Haarzellen Schleim ab, welch’ letzterer bei der Quellung im Wasser gleichsam ausgestossen wird. Auf diese Weise umgibt sich die Frucht mit einem klebrigen

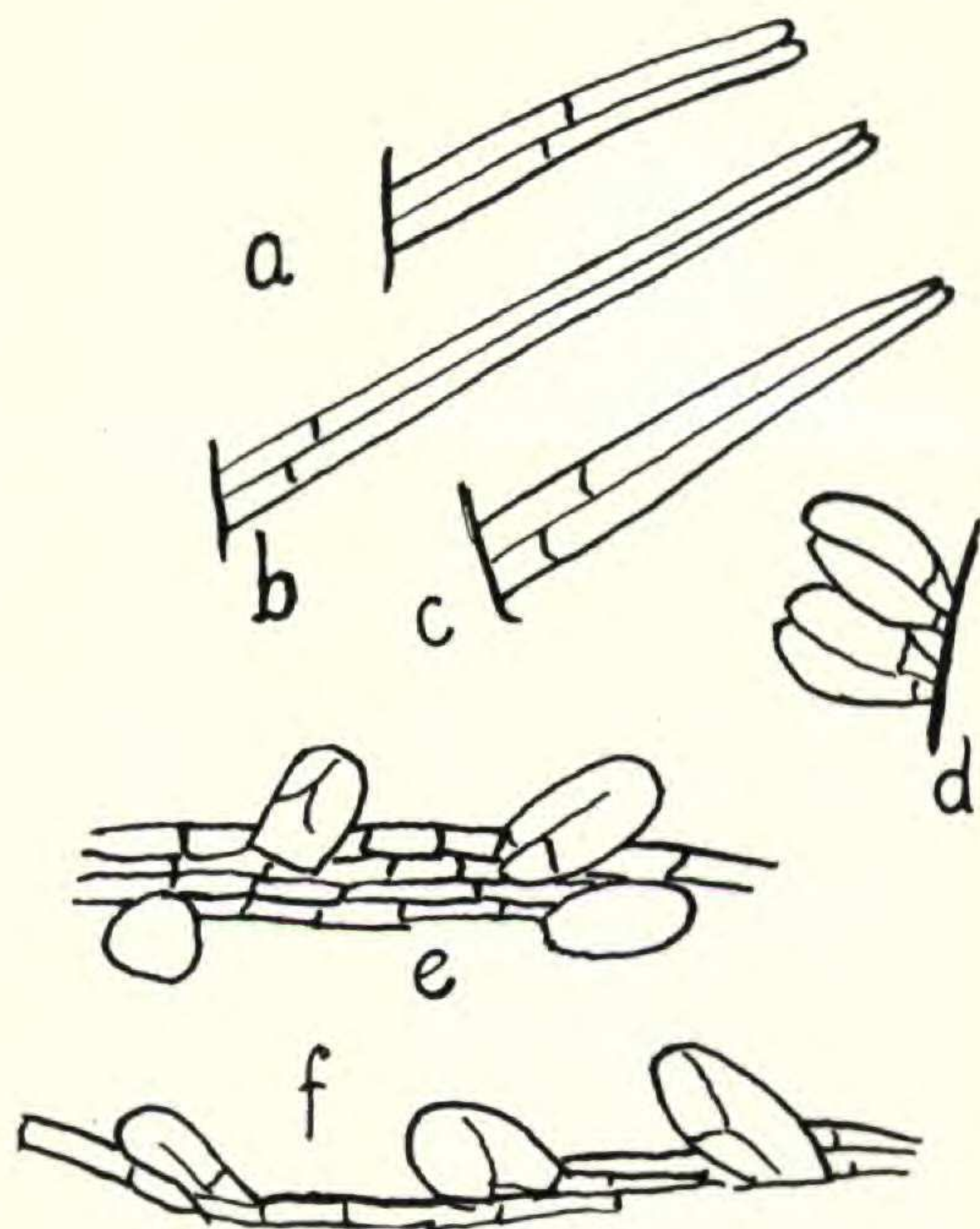


Fig. 4. Achenial Hairs swollen, a: of *GNAPHALIUM NORVEGICUM*; b: of *G. SUPINUM*; c: of *LEONTOPODIUM ALPINUM*; d: of *FILAGO ARVENSIS*; e and f: of *ANTENNARIA PETALOIDEA*, young staminate plant; all $\times 133$.

Ueberzug, wodurch ein Festkleben der Achaenen an der Unterlage ermöglicht wird.” From the quotation it cannot be seen whether this refers to an actual observed case or is merely a conjecture *per analogiam*. In our case such a function probably cannot be of much importance considering the minuteness of the mucilage drops in proportion to the size of the achene. A great number of species, probably the greatest part of the genus, have totally glabrous achenes and do quite as well. And I may here add that the abortive ovaries of the staminate plant of *A. petaloidea* also carry twin hairs, see FIG. 4, e and f. My

material was very young, taken before the corollas were expanded, so I cannot tell whether the hairs will develop to normal size and form. Here at least there cannot be such a function. Undoubtedly the hairs are an old character inherited from ancestral forms and in this connection it is interesting that fertile and apogamic species occur in both groups, those with hairs and those without.

JAMES SMALL as well as the authors he refers to seems to be fairly convinced of the importance of the occurrence and the form-types of the achenial hairs in questions of interrelationship and evolution. Having, in Greenland, no access to the extensive literature on the subject, the present writer is unable to compare the conditions found in *Antennaria* with the cases known before. I could only look over the achenes of some genera and species which, according to the adopted taxonomy, are considered near relatives of *Antennaria*. And as my herbarium generally consists of specimens from Arctic or Alpine regions only, the suitable material was sometimes rather defective.

GNAPHALIUM.

The achenes of the boreal Old World species are partially described in the leading floras. Of these *G. arenarium* and *G. luteoalbum* would seem especially inviting for our purpose, but they are not at hand. The achenes are characterized thus:

	HARTMAN: Handb. Fl. Sk. 1879	ROUY: Fl. de France. Vol. 8	HEGI: Illust. Fl. Mitt.-Eur.
G. ARENARIUM	glatta, grynprickiga	0	sehr feinknotig
G. LUTEOALBUM	0	glabres, chagrinés	etwas rauh
G. ULIGINOSUM	sl"ta, glatta	0	glatt
G. SUPINUM	glest str"fhåriga	pubescents	kurzhaarig
G. SILVATICUM	småhåriga	0	kurzhaarig
G. NORVEGICUM	"	0	sp"rlich behaart

The achenes of *G. uliginosum* are, as said, totally smooth and glabrous, differing widely from the three following ones. In the last three species they are conspicuously pubescent with straight, slightly ascending hairs. In the swollen state the upper parts of the hairs are glassy-hyaline, and by enlargements from 200 \times upwards a longitudinal division is seen (see FIG. 4, a and b). In *G. supinum* the pubescence is remarkably denser and the individual hairs longer, 0.13–0.15 mm., whereas in *G. silvaticum* and *G. norvegicum* they are 0.08–0.09 mm. only. The difference in the density suggested by HEGI I cannot see, nor is it noted in other Scandinavian floras. Also here the trans-

verse cells are not opposite, just as in *Antennaria*. Even after several days swelling no splitting of the terminal cells occur and no mucilage is seen. The hairs are thus evidently “duplex-hairs” but different in type from those of *Antennaria*.

The achenes of *Leontopodium alpinum*, by HEGI called “rauh,” carry twin hairs of exactly the same type as *Gnaphalium*, 0.08–0.09 mm. long and perhaps slightly thicker (see FIG. 4, c). As in *G. supinum* the lower part is much shorter than the upper.

ANAPHALIS MARGARITACEA var. SUBALPINA. The young and quite immature achenes carry a dense covering of short, 0.05 mm. long, twin-hairs of the *Gnaphalium* or *Leontopodium* type.

The following species would, judging by the descriptions given, probably be inviting objects for comparison, but are unavailable here:

	HARTMAN	ROUY	HEGI
HELICHRYSUM ARENARIUM	0	chagrinés	sehr feinknotig
HELICHRYSUM ITALICUM	0	0	warzig rauh
FILAGO GERMANICA	hvitprickiga	finement glanduleux	0
FILAGO GALLICA	0	0	mit dicken glashellen Warzen besetzt

Instead I have studied mature achenes of *Filago arvensis*, of which nothing is said in the floras, but which in dry state would agree well with HEGI’s description of *F. gallica*: covered with coarse, hyaline warts. Indeed they are a coarser representation of the “papillose” achenes in *Antennaria*. When swollen they appear like FIG. 4, d, often growing in clusters of twos or threes, which in drying shrink together to form the “wart.” They project only 0.04–0.05 mm. from the epidermis.

Amongst the few species studied we thus found the achenial hairs most similar to those of *Antennaria* in a genus which in the adopted system is not considered the nearest relative of our genus.

At the end of this little investigation the author realizes too well its defectiveness. Yet, he hopes that the results obtained will suggest that the achenes of the great number of *Antennarias* already described and of those still to be proposed as new may be scrutinized for their achenial hairs and that investigations of the organs in related or ancestral genera may be taken up where ampler material and literature are at hand. The fact that glabrous and “papillary” species exist, both in great numbers, may perhaps suggest a polyphyletic origin

of the genus as we now understand it. The high number of chromosomes known for *A. dioica* and *A. alpina* also seem to speak for hybridogen origin.

DISKO, GREENLAND.

THREE ANTENNARIAS FROM GREENLAND¹

M. L. FERNALD

ANTENNARIA affinis, n. sp., humifusa, stolonibus foliosis (ad 4 cm. longis); foliis basilaribus spathulato-cuneatis apice subtruncatis vel late rotundatis vix mucronatis 6–13 mm. longis 2.5–6 mm. latis utrinque albidis pannoso-tomentosis; caule florifero 3–14 cm. alto; foliis caulinis 6–9 subdistantibus, imis anguste oblanceolatis obtusis, mediis linearibus acutis mucronatisque 8–13 mm. longis 2 mm. latis, superioribus 1–2 apice subscarioso subulato vel involuto 0.5–1 mm. longo munitis; capitulis femineis 1–15 dense corymbosis vel glomerulatis turbinato-campanulatis; involucri 5–5.5 mm. alto basi lanato subviscoso; bracteis 2–3-seriatis margine erosis, exterioribus late oblongis obtusis stramineis basi fulvescentibus, interioribus lanceolatis acutis apice ochroleucis; corolla 4–4.5 mm. longis, apice purpurea; stylo incluso vel vix exserto; achaeniis 0.8 mm. longis minute papillosis; foveis receptaculi ovoideo-conici maturi denudati 60–100 0.1 mm. latis quam jugis separantibus obtusis latioribus; planta mascula ignota.—GREENLAND: Ipiutarssuaq, 67° 42', August 5, 1918, *M. P. & A. E. Porsild* (TYPE in Gray Herb.); on basaltic moraines, S. Disco, Sinigfik, 69° 25', August 12, 1929, *R. T. Porsild*; Kûk ("Kome"), 70° 36', July 26, 1921, *A. E. Porsild*; sunny ledges, Agpat-formation, Umánaq Storø, Paornat, 70° 40', July 8, 1929, *M. P. & R. T. Porsild*; Umánaq, August 25–30, 1923, *Elizabeth Ekman*; on sunny ledges of the Agpat-formation, Upernavikø, 71° 15', July 14, 1929, *M. P. & R. T. Porsild*; Upernavik, 71° 20', July 23, 1921, *A. E. Porsild*; all the Porsild collections distributed as *A. subviscosa* Fernald.

As stated, *Antennaria affinis* was distributed as *A. subviscosa* Fern., but it is not satisfactorily identified with the latter species which is known only from Bic, Rimouski County, Quebec, and from three stations in Gaspé County (Marsouin River, Cap Pleureuse and Gros Morne), where, with other relic species, it occupies shelves of vertical

¹ At the request of the late Professor Ostenfeld the description of the first species was sent to him for publication in Denmark. Owing to Dr. Ostenfeld's most regrettable and untimely last illness publication of the paper was overlooked. Dr. Porsild has most kindly supplemented the original material by beautiful specimens of additional numbers, as well as by two other species heretofore unknown in Greenland. One of the latter is here described; the other, too mature for exact identification, must await younger specimens.